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THE GRASS GENERA ORCUTTIA AND NEOSTAPFIA: A STUDY IN HABITAT AND MORPHOLOGICAL SPECIALIZATION

BEECHER CRAMPTON

Without a doubt, the endemic genera *Orcuttia* and *Neostapfia* are the most unusual and rarest of the California grasses. *Orcuttia* comprises five species and two varieties, while *Neostapfia* is monotypic. All are narrowly restricted annuals which develop in the summer beds of vernal pools and exhibit peculiar morphological features. Their relationship to other grasses is not apparent and quite likely they represent a relict group, the ancestors of which are unknown. Very few collections of them had been made up to the time Hoover (3) made known the degree of speciation and geographical range of the *Orcuttia* species. A relatively small number of these grasses has been collected since.

In cooperation with the Department of Agronomy, University of California, Davis, and its grass research program, the author was privileged to spend part of the summer of 1958 observing the nature of the habitat and making extensive collections of these fascinating grasses. The results were very gratifying, and the success of this specialized exploration has prompted the author to present his findings and to provide additional information about the habit, habitat, and morphological development of these two unique genera in the California grass flora.

The author is especially grateful for the helpful suggestions and criticisms by Dr. G. L. Stebbins, Department of Genetics, and Dr. Jack Major, Department of Botany, both of the Davis campus, University of California.

I. THE NATURE OF THE HABITAT

While many of the Californian grasses are relatively unspecialized as to habitat, *Orcuttia* and *Neostapfia* are restricted to vernal pools. These basins, sometimes called "hog wallows," are best developed on the rolling plains surrounding the Great Valley of California, and to a lesser extent on the valley floor. Rainwater collects in them and stagnates during the winter and spring, and by late spring or early summer it has completely evaporated. The pools are quite variable in extent or area, depending upon the terrain. Some are small, shallow, or circular to irregular shape, and several meters in diameter. Others may be greatly ramified, with numerous islands, while some are quite large, perhaps 500 meters or more in diameter, being then classed as intermittent lakes.

Upon evaporation, the recession of the water from the margin initiates development of a unique flora on the muddy strand. Some plant species, however, depend upon the standing water for seedling development or renewal of perennial growth. It is not unusual to find mature annuals on the margins of the pools, while very young plants of the same species are in active growth at the edge of the receding water. Such annual plants

as *Allocarya*, *Pogogyne*, *Downingia*, and *Navarretia* often show this pattern and become generally distributed over the beds. The grasses, *Deschampsia danthonioides* and *Hordeum hystrix*, are restricted to the margins. Of the perennials, *Eryngium* may be generally distributed or marginal, while *Eleocharis palustris*, *Marsilea*, and sometimes *Damasionium* are in the central or deeper portions of the basins. The distribution or occurrence of any one plant species in this environment is quite dependent upon size, depth, and soil type of the pool and the length of time of standing water.

Orcuttia and *Neostapfia* require a very special type of vernal pool. The concept of "hog-wallow" should be amended to "elephant-wallow" to satisfy the environmental demands of these grasses. Primarily, the optimum size of their vernal basins is about 20–100 meters or more in diameter or length. Secondly, such basins must neither be drained naturally nor artificially, for long periods of standing water are a necessity. Dry, unfavorable years result in a paucity of the grasses, while years of heavy rainfall such as 1958 (Table 1) are responsible for their peak development. The best stands of either *Orcuttia* or *Neostapfia* occur mostly in the absence of other vegetation (fig. 1E). The adobe muds in the large vernal pools, with their barren, dried, cracked, and often well trampled surfaces, are ideal sites. The presence of the ubiquitous vernal pool *Eryngium vaseyi* and the sedge, *Eleocharis palustris*, restricts the density of *Orcuttia* and *Neostapfia*. Any dense stand of either of these perennials has relatively few to none of the annual grasses among them. Barren areas or clearings in *Eleocharis* and thin stands or absence of the *Eryngium* become excellent sites for *Orcuttia* development. *Marsilea* apparently has no deterrent effect on the grasses, as it is a frequent associate of them. Relatively few annuals offer competition to *Orcuttia* or *Neostapfia*, *Boisduvalia* being probably the commonest, with occasionally *Eremocarpus* and certain *Euphorbia* species, but in the main most annuals have dried before maximum development of the grasses occurs.

Recognition of the proper habitat of *Orcuttia* and *Neostapfia* simplifies collection of these unusual grasses. The most numerous, shallow, early drying vernal pools can thus be eliminated as sites for their occurrence, and only the large-type pool, with some barren portions, need be considered.

In the past evolutionary history, *Orcuttia* and *Neostapfia* probably developed as shore or strand grasses on the margin of a sea, such as once covered the present Great Valley area. The conversion of the sea to a land surface involved only minor modification in the character of the habitat so that isolated ponds, developing along the shore of the receding sea, became an eventual refuge for these grasses. Perhaps the greatest change came in elimination of salts, yet *Neostapfia* has been found growing on alkali in Colusa (the type locality) and Solano counties. *Orcuttia mucronata* occurs, as far as is known, only on alkali, but other species of the genus favor nearly neutral or perhaps slightly acid soils. It also became

necessary for the plants to withstand the period of summer dryness as developed in the Great Valley and surrounding areas during the geologic changes.

II. THE AREAS OF COLLECTION

The pioneer work by Hoover (3) established geographical ranges for the species of *Orcuttia* and enabled the present writer to visit several areas of known occurrence of these narrow endemics. Aside from studying habitats and associations, extensive collections were made of all species except *Orcuttia californica*, which occurs only in southern California.

A. THE SAN JOAQUIN VALLEY

1. Stanislaus County. The low hill and rolling plain areas bordering the Tuolumne River east of Waterford and Hickman, are especially rich in *Orcuttia* and *Neostapfia*. The topography favors development of the larger-type vernal pool. In this region the upland soils are primarily a reddish loam of the San Joaquin series, while the pool beds are light to dark grey adobe of the Alamo series, well permeated with iron compounds which act as cementing materials. Most of the land is grain-farmed, some exists as dry rangeland, while other areas have been converted to irrigated pasture.

In the grainfields between the southern part of Modesto Lake and State Highway 132, there are seven large vernal pools bordering on Dienstag and Reservoir roads. All but one of these basins had excellent stands of *Neostapfia*, four of them with abundant *Orcuttia pilosa*, and a single one with *Orcuttia californica* var. *inaequalis*. Hoover apparently overlooked this particular area of *Orcuttia* and *Neostapfia* while collecting in 1936–1938. The type locality for his *Orcuttia pilosa* lies five miles farther east, the region, as far as determinable, now being irrigated pasture.

Two vernal basins border Dienstag road, the southern one unequally divided by the gravel roadbed (fig. 1-A). The larger and western section of this latter pool is about 100 meters across at the widest point and nearly 125 meters long. Its basin was entirely covered by a magnificent, dense stand of *Neostapfia* (fig. 1-B). A few scattered clumps of *Eleocharis palustris* and *Sida hederacea* were found along the fence adjacent to the road, otherwise there was pure *Neostapfia*. The green "sheet" of this grass was in marked contrast to the dry barley stubble on the surrounding slopes.

The eastern and smaller portion of this vernal pool is bordered by hilly rangeland. At the lowest point, near the road, there was still some standing water on July 28, 1958 (fig. 1-A). Surrounding the murky water, in a semicircle, was a wide band of barren, dark-grey, well-trampled mud. On the periphery of the mud, a pale green band of *Neostapfia* was developing on the cracking, drying, grey adobe. Several resident dairy heifers were intermittently, but actively grazing the grass!

The second vernal pool along Dienstag road is about 100–125 meters long and perhaps 75 meters wide. The bed was a solid stand of *Neostapfia*

with an abundance of *Orcuttia pilosa* along the margin. This unique pattern invariably occurred whenever the two grasses were associated.

Three vernal pools along and south of Reservoir Road were replete with *Neostapfia* and *Orcuttia pilosa* as the sole or major occupants. One pool, however, contained mostly *Orcuttia californica* var. *inaequalis*, very little *Orcuttia pilosa*, and no *Neostapfia*. Another pool was of unique shape, nearly 150 meters long and about 10 meters wide, its bed a pure, solid stand of *Neostapfia*.

The barley field operations in this area apparently do not affect the successful development of these peculiar grasses in their habitat. Undoubtedly the planting machinery disturbs the vernal pool beds in the fall, yet after that they remain undisturbed until harvest, at which time *Orcuttia* and *Neostapfia* are reaching maximum development.

A large playa, about 150 meters or so in diameter, is situated in a small valley leading out of the hilly country three miles east of Hickman. Though the surrounding areas are grain-farmed, the vegetation of this bed differs considerably from those of the previous area. *Neostapfia* is restricted to small patches, while *Orcuttia californica* var. *inaequalis* is more widely dispersed. Active competition is afforded by *Centromadia fitchii*, *Boisduvalia*, and *Eryngium*, with an abundance of dried *Allocarya*, *Downingia*, and *Navarretia leucocephala*. The more barren areas on the dried and cracked lead-grey adobe support the best stands of both *Orcuttia* and *Neostapfia*.

An extensive reservoir or permanent lake¹ (fig. 1-C) is located on the Loren Rouse Ranch six to seven miles east of Hickman, along the road to La Grange. *Neostapfia* and *Orcuttia pilosa* occur abundantly along the strand, which is subject to vernal flooding and summer drying. This lake has quite likely been developed from a large vernal playa which originally was populated by these two grasses, since the margins of man-made reservoirs are not ordinarily sites for development of either of these grass genera. If planted, they might very well become adapted to reservoir strands.

Summer fallowing of the hilly grainland to the south had closely approached, nevertheless had not disturbed the strand. Dry rangeland and irrigated pasture surround the lake on the north and east, respectively, though neither operation had disturbed the habitat.

The old Paulsell warehouse is located along the old Sierra railroad northeast of Waterford. The land area is now largely devoted to irrigated pastures except for the hilly, dry rangeland to the north. The distinctive *Orcuttia greenei* was found in a large, undisturbed playa at the southwestern base of a prominent knob-like hill. The playa basin is perhaps 200-250 meters in diameter and composed of black, deeply-cracked adobe. Aside from the dense, dried *Allocarya* cover, *Eryngium* and *Eremocarpus* were dominant, with some *Eleocharis palustris* and *Boisduvalia*.

¹ Since the above was written, it has been learned that this is a natural pool.

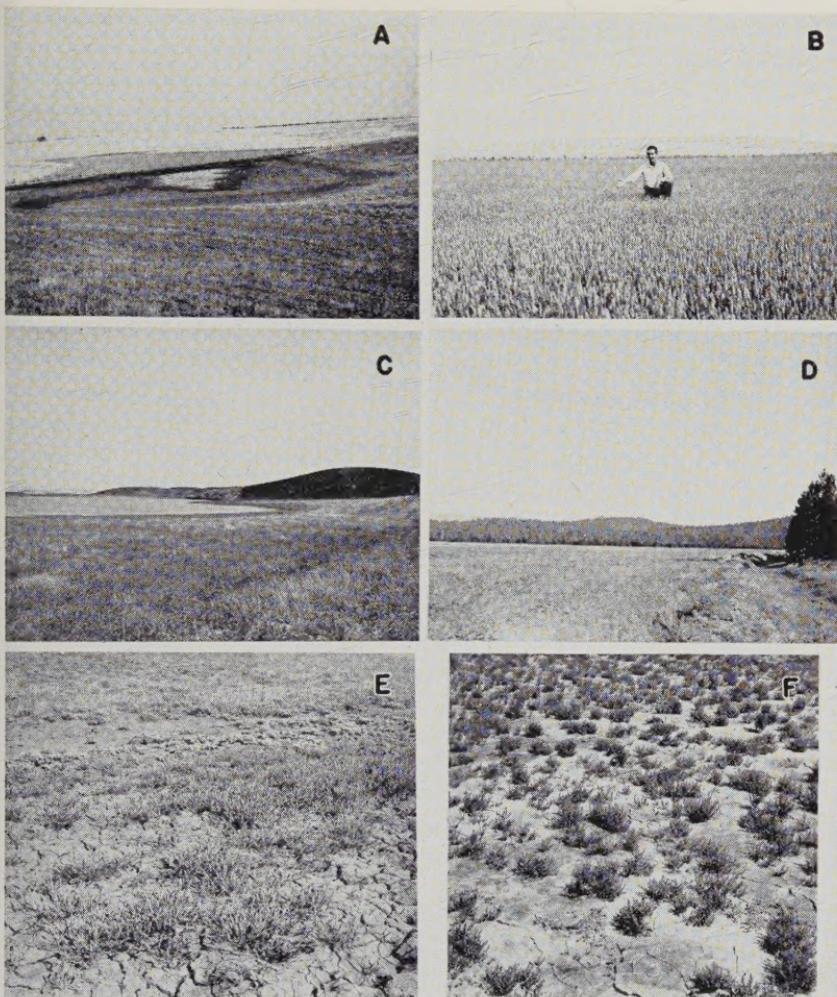


FIG. 1. The habitats of *Orcuttia* and *Neostapfia*. (A) Large vernal pool in the barley-farmed area south of Modesto Lake, east of Waterford, Stanislaus County. Dienstag Road divides the basin. (B) The author in the solid stand of *Neostapfia* present in the far portion of A. (C) Lake on the Rouse Ranch east of Hickman, Stanislaus County, the strand of which has an abundance of *Neostapfia* and *Orcuttia pilosa*. (D) Goose Valley, Shasta County, the type locality of *Orcuttia tenuis*. The author collected the grass in the ditchbed at the right. (E) *Neostapfia* growing on a typical soil of a vernal pool bed. Note the cracks and absence of other vegetation. *Eremocarpus* lines the bed in the background. (F) Habitat of *Orcuttia mucronata*. *Frankenia* and the prostrate *Eryngium aristulatum* are the only associates.

The *Orcuttia* was not abundant, but occurred mostly as scattered plants in areas containing the least *Eryngium* and *Eremocarpus*.

2. Merced County. In the vicinity of the old Ryer station, located 6.5 miles south of Montpelier, there are two large-type vernal pools containing *Orcuttia californica* var. *inaequalis*. The rather uniform rolling hill country in this area is all grain-farmed, with rather numerous, smaller-type vernal pools. The large playa to the west is basically a lead-grey colored adobe, well populated with *Centromadia fitchii*, *Centromadia pungens*, *Sida hederacea*, *Boisduvalia* and marginal *Eryngium* as well as the dried *Allocarya*, *Downingia* and *Navarretia leucocephala*. The *Orcuttia* was most abundant in areas of the least competition.

The eastern vernal pool harbored a dense stand of *Orcuttia californica* var. *inaequalis* to the near exclusion of other plants. Apparently the basin had been completely cultivated during barley planting, for faint furrows were evident over the pool bed. The *Orcuttia* was exceedingly robust, some of the plants being 12–15 cm. high and with as many as 60 culms, a development far in excess of those in the neighboring playa. Aside from dried *Allocarya*, only a few scattered plants of *Centromadia* and *Eremocarpus* were present.

North of Legrand, in typical rolling plain rangeland, is a large playa perhaps 300–350 meters in diameter. The soil of the basin is a black adobe, becoming exceedingly deeply cracked when dry. Some of the cracks extended from three-fourths to nearly a meter in depth and from 5–10 cm. across at their aperture. A dense stand of *Eremocarpus* covered the major portion of the bed, the whole appearing from a distance as a silver-grey "lake." Large specimens of *Orcuttia greenei* were numerous in areas of the least *Eremocarpus*, though scattered individuals occurred throughout the playa. *Boisduvalia* was perhaps the closest and only other associate.

B. THE SACRAMENTO VALLEY AND NORTHERN CALIFORNIA

1. Solano County. A magnificent alkaline, intermittent lake is situated in a rolling plain area twelve miles south of Dixon, Solano County. It is shallow, has no drainage, and is about 500 meters in diameter. The predominant vegetation in the lake basin is *Frankenia grandifolia*, *Cressa truxillensis*, *Sida hederacea* and *Eryngium aristulatum*, with some patches of *Eleocharis palustris*. The marginal strand is largely *Distichlis*, *Lippia* and *Navarretia bakeri*. The dried crust varies from a uniform, glaring-white pavement to a tan and cracked surface. On the latter type, *Neostapfia* and an undescribed species of *Orcuttia* grew in association with *Frankenia* and *Eryngium* (fig. 1-F). Both grasses, at their best, were rare occupying an exceedingly small area of about 15–20 meters in diameter. The *Orcuttia* will be described later in this paper as *Orcuttia mucronata*, while the occurrence of *Neostapfia* here represents a new area for California.

2. Sacramento County. According to Hoover (3), *Orcuttia californica* var. *viscida* is not known to occur outside of Sacramento County. The Orangevale area now shows a distinct waning of the grass, and in all probability the habitat will be eliminated by residential development.

On the higher, rolling plains north of Sloughhouse, one large vernal pool and several smaller, but deep ones, support fairly good stands of this attractive *Orcuttia* and represent its type locality. It was conspicuous along the margins and in some parts of the bed of the large pool. This greater basin, 100 or more meters in length and with some ramification, is largely a barren and stony bed. The cracked, lead-grey, adobe soil is well supplied with iron concretions, apparently an indication of the type of soil several *Orcuttia* species prefer. Some patches of *Eleocharis palustris* and *Eryngium* were present, but these species were certainly not diffuse in any area of the pool.

3. Butte County. A single vernal pool on the rolling plains about ten miles southeast of Chico was well supplied with *Orcuttia greenei* and probably represents the type locality of this species. The basin, 75-100 meters in diameter, is composed of a grey-black, crumbly, stony, and pebbly soil. Over the major portion of the pool the marginal vegetation of *Eryngium* and *Eremocarpus* gave way to an abundance of the *Orcuttia* and to the prostrate annual *Euphorbia hooveri*.

4. Tehama County. *Orcuttia tenuis* is endemic to northern California, preferring soils probably derived from volcanic substrates. Only certain areas of Tehama, Shasta, and Lake counties have the proper environmental conditions, each of them in entirely different settings.

In Tehama County, on a rocky, volcanic plateau eleven miles northeast of Red Bluff, lies an extensive dry lake known as Hog Lake. The basin is perhaps 300 meters wide and 1500 meters long, surrounded by mixed, open grassland and blueoak woodland. The western shallow portion and the marginal strand were largely populated by *Eryngium*, while the deeper portions contained *Eleocharis palustris* and *Damasonium*. The best development of *Orcuttia tenuis* occurred in the barren, stony areas among patches of the *Eleocharis* and to a lesser extent *Damasonium*. Although the grass was rather uniformly distributed among *Eryngium*, it had dried too quickly here for proper seed set. The dried, leached grass stood in marked contrast to the grey-green plants in anthesis and fruit maturation which occurred in the deeper and barren areas of the lake basin.

5. Shasta County. *Orcuttia tenuis* occurs in abundance in a series of vernal pools around the Redding Municipal airport three to five miles north of Anderson, the area being known as Stillwater Plains. The southern series is largely in open grassland, while those to the west and north of the airport are surrounded by oak, digger-pine, and manzanita. The typical floristic association pattern of all of the pools can be illustrated by that in a single pool, a circular basin about 125 meters in diameter. Here *Eryngium* is marginal, but the majority of the bed contains *Eleocharis palustris* with intermittent patches of *Marsilea*. Although some of

the *Orcuttia* grew among the sedge, it was more common in the barren situations. None of the grass could be found among the *Eryngium*.

Two shallow and smaller pools associated with the open grassland had evidently dried too quickly, for the grass was leached and the spikelets were without seed. A small but deep ditch along the road and continuous with one of these basins contained green and properly maturing *Orcuttia*.

The type locality of *Orcuttia tenuis* is Goose Valley, north of Burney, Shasta County. The type collection was made here by Alice Eastwood in 1912, and since that time no other collections are known to have been made. This mountain valley is around 3500 feet in elevation, surrounded by mixed conifer forest, and is primarily meadowland with some dry-lake habitats in the northern section. Most of the valley is now largely cultivated, either as permanent pasture or cropland. A series of canals which effectively drain many areas is consequently disastrous to the survival of the *Orcuttia*. Fortunately, the grass was located in the nearly barren bed of an old ditch skirting a northeast portion of the valley (fig. 1-D). Aside from small patches of *Eleocharis palustris* and *Damasonium* along the edges, and some scattered *Downingia* and *Boisduvalia* in the bed, *Orcuttia tenuis* remained the dominant plant of the basin.

6. Lake County. The occurrence of *Orcuttia tenuis* in the Coast Ranges was first made known by Milo Baker, eminent Santa Rosa botanist, who collected the grass on the north shore of Bogg's Lake, Lake County. This lake is situated in a yellow pine forest flat on the northwest slope of Mount Hannah. The basin is around 1650 meters in diameter, contains water the year round, yet is provided with an adequate strand for the development of many unique and unusual plants.

A visit to the lake in August, 1958, proved disappointing because of the high water level and resultant flooded strand. Previous to 1958 the author had collected the grass on the southwest margin among *Eleocharis palustris* and *Eryngium* though it was exceedingly rare, requiring considerable search to locate perhaps two dozen plants.

III. YEARLY FLUCTUATIONS IN ABUNDANCE

The year 1958 was an ideal one for maximum development in the stands of *Orcuttia* and *Neostapfia*. In all of the areas visited, with one exception, these grasses were abundant, the most remarkable being the magnificent stand of *Neostapfia* just south of Modesto Lake.

What of other years? Even though the grasses must, in the overall floristic analysis, be regarded as rare and narrowly restricted endemics, why have they not been collected more often? The answer undoubtedly lies in their fluctuations in abundance from year to year. Unfavorable, dry years would be associated with poor development or scattered stands and earlier maturity. A shallow depth of water evaporating rapidly during the spring might prove quite disastrous to the annual stand of the grasses, even though they are situated in the required habitat. Such an environmental stress would antagonize the genetically-fixed, summer-

maturity character of *Orcuttia* and *Neostapfia*, resulting in heavy seedling mortality and consequent rarity of plants in the habitat. Furthermore, supposing good germination in water or on the mud of the vernal basins, too rapid a drying might cause premature flowering and poor to no seed set.

How, then, is perpetuation of the grasses maintained over unfavorable periods? Presumably the large seed production effected in such a year as 1958 might be adequate for the next several years, since there is a suggestion that the seed remain viable over many years and that a prolonged period of dormancy may be necessary before germination occurs. This supposition is drawn, but perhaps too hastily, from an attempt to germinate *Orcuttia* seed. *Orcuttia pilosa* grains collected in August, 1957, were placed on a blotter in a petri dish on January 31, 1958, kept at room temperature, and under continuous moisture. By September 1, 1958, no germination had occurred, though very few of them had succumbed to mold. Aside from the moisture, this artificial medium lacks all of the elements of the natural ones.

TABLE 1. Annual Precipitation (July to June) of four reporting stations in the Great Valley of California*

Season	Merced	Modesto	Sacramento	Red Bluff
1931-1952 (average)	12.35	12.44	16.68	23.15
1955-1956	15.42	15.62	25.53	28.53
1956-1957	7.40	8.63	13.78	12.25
1957-1958	25.63	23.04	28.70	38.03

* Data obtained from USDA Weather Bureau-Climatological Data, California section.

Table 1 shows some climatological data for most of the areas where the writer collected *Neostapfia* and *Orcuttia* in 1958. The amount of rainfall during the 1957-1958 season supports the argument that abundance of the two grass genera is dependent on the amount of precipitation. In all probability there was generally minimum development of the grasses during the 1956-1957 season. Dr. G. L. Stebbins, department of Genetics, and Dr. and Mrs. Louis Mann, department of Vegetable Crops, University of California, Davis campus, visited the vernal pool as shown in Figure 1-A, in the latter part of June 1957. They could scarcely find any *Neostapfia*, and what few plants were found were thoroughly dried and mostly dessicated. The remarkable solid stand of the grass present in July, 1958, could not have developed from the 1957 crop. Undoubtedly a larger seed crop had been produced in previous and more optimum years.

Without doubt, judging by observation of the excellent stands of both grass genera in 1958, the amount of rainfall and consequent depth of standing water in the vernal pools is most critical in their life cycle and reflects their yearly abundance.

The collections by Hoover (3) and others have pretty well established the geographical range of the *Orcuttia* species and *Neostapfia*. It remains

to round out their distribution by detailed collections of the two genera from year to year.

The primary purpose of this paper has been to stimulate interest in these most unusual and scientifically interesting grasses and make known their specific type of habitat and specific locations. The progress or decline of the grasses in any one area can be evaluated by the frequency of collection. This concern by the author is not without foundation. With the steady increase in California's population and with the resulting modified land manipulation that must occur, there is a good possibility of the destruction of many habitats, and this may result in the extinction of these grass species or their varieties.



FIG. 2. *Orcuttia mucronata* sp. nov. Plant from type specimen, approximately natural size.

IV. AN UNDESCRIPTED SPECIES OF ORCUTTIA

The extensive collections of *Orcuttia* and *Neostapfia* made during July and August, 1958, uncovered a most unusual and distinctive *Orcuttia* species on the western side of the lower Sacramento Valley. The grass differs rather considerably from most other *Orcuttia* species, and a more radical treatment might erect a new genus. However, until all details of the plant can be evaluated it seems expedient to assign the grass to *Orcuttia*.

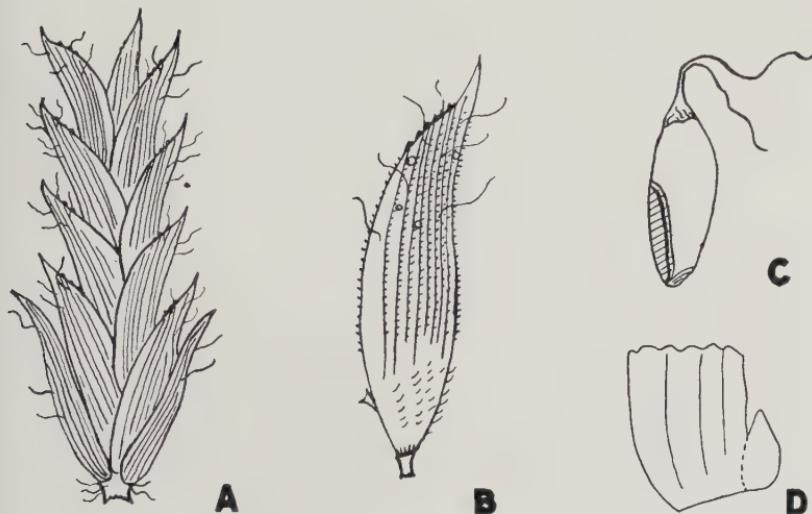


FIG. 3. *Orcuttia mucronata* sp. nov. (A) spikelet, $\times 5.5$. (B) floret, $\times 7.3$. (C) caryopsis, $\times 7.3$. (D) lodicule fused to the palea, $\times 18$.

***Orcuttia mucronata* sp. nov.**

Planta annua aestivalis aromatica flavoviridis folia rigida extrinsecus curvata 1–4 cm. longa inflorescentia racemiformis basi tantum inclusa spiculis 7–19 spiralibus 5–10 floribus nec supra nec infra glumas disarticulantibus lemmis 5–7 mm. longis apice mucro unico terminatis dentibus lateralibus suppressis palea apice trilobata lobis dentatis lodiculis duabus hyalinis enervatis paleae adnatis.

Summer annual; pilose throughout, yellow-green, aromatic. Culms few to many, decumbent, 2.5–12 cm. high; leaves eligulate, viscid, 1–4 cm. long, somewhat rigid, curved outward tapering to a fine point; inflorescence a raceme, 1.5–6 cm. long, partially included, spikelets 7–19 in number, spirally arranged; spikelets 7–13 mm. long, 5–10-flowered, no disarticulation between the florets or below spikelet; glumes 4–7 mm. long, unequal, nearly approximate, lanceolate, the apex pilose, mostly awn-pointed or occasionally with 1 or 2 lateral teeth; lemmas coriaceous, 5–7 mm. long, the upper portion excurved, sparsely pilose, scabrous, viscid and light green, the lower portion short-hairy and whitish, the apex obtuse with a median mucro, 0.5 to nearly 1 mm. long, the lateral teeth suppressed, the margin appearing merely erose; palea shorter than the lemma, the apex 3-lobed, the lobes toothed, pubescent towards the margin near the apex; lodicules 2, fused to the palea, hyaline, nerveless, about 0.25 mm. wide and 0.5 mm. long; anthers yellow fading pinkish; caryopsis oblong, flattened, 3 mm. long, the embryo 1.5–2.0 mm. long along one side of the grain (figs. 2 and 3).

Type. Alkaline lake, 12 miles due south of Dixon, Solano County, California, August 1, 1958, Crampton 5057, AHUC. (Isotypes: UC, JEPS, DS, US, CAS, K.) Known only from a single dry lake at the type locality.

Other collections (Crampton 5011, 5059, 5093, and 5113), all collected in this single locality, represent a series of developmental stages. *Orcuttia mucronata* is, at the most, rare. Only three patches of the grass, roughly 3–8 meters in diameter have been found over the large expanse of the lake bed. These small populations apparently occur in the deeper portions and on a cracked alkali with a brownish film over its surface. The white, smooth alkali pavement, characteristic of much of the lake harbored none of the grass. The soil type is classified as the Lindsey clay loam series. The soil survey of the Suisun area (1) indicates that the surface of this soil is a dull, dark or brownish grey material with a large proportion of fine to very fine sand. It deflocculates and when dry it becomes hard and baked. Organic matter is low, and most areas contain alkali. During the rainy season such areas become ponded for weeks or months at a time, the soil taking water slowly and having a high water-holding capacity. The surface layer extends from 8–10 inches in depth, and certain areas contain lime. The subsoil is heavy textured and compact, with some calcareous areas.

The soil at the area where the type plants of *Orcuttia mucronata* grow shows a pH of 8.0 on saturated paste as determined by the Agronomy Soils Laboratory.

V. MORPHOLOGICAL CHARACTERISTICS

The classical alliance of *Orcuttia* and *Neostapfia* to the tribe Festuceae, on the basis of gross spikelet morphology as outlined by Hitchcock and Chase (2), is inadequate in establishing relationship of the two genera to other grasses. A review of the salient features of both *Orcuttia* and *Neostapfia* indicates that they are not closely related to any members of the Festuceae.

One of the most conspicuous features of these grasses is the viscid secretion on all aerial parts of the plant whether young or mature. At first the secretion is glistening and watery, but towards maturity it becomes a thicker, denser, usually brownish exudate. In *Neostapfia*, distinctive scale-like raised glands on the lemma nerves and leaves contribute to the viscosity. In association with the copious secretion, a peculiar odor emanates from either fresh or dry material in any stage of development. The viscosity undoubtedly conserves plant moisture during the warm late spring and hot summer temperatures, while the aromatic habit may serve to reduce or repel animal depredation. In some of the collection areas grasshoppers were in abundance, but the green *Orcuttia* or *Neostapfia* plants were unaffected by the voracious insects.

In marked contrast to the Festuceae, *Orcuttia* and *Neostapfia* are summer-maturing annuals that occupy a highly specific type of habitat. Their coloration varies from a pale- to grey-green, and all are hairy. In

Neostapfia, however, hairs on the foliage are sparser, and very minute.

The nature of the foliage is distinctive, for in both genera there is no differentiation into sheath and blade, and consequently a true ligule and well-defined collar are absent. In all but *Neostapfia* and *Orcuttia mucronata* there is a definite abscission of the blade portion of the leaf. This deciduous character is not apparent until the leaves are dry, although in some instances the point of abscission is faintly visible in green tissue and might correspond to a "collar." The hairiness on the upper surface of the *Orcuttia* blades terminates abruptly at the fracture region, so that the resultant line of hairs might be construed as ligular. Otherwise the leaves of both genera loosely envelope the culms.

The culms of *Orcuttia* and *Neostapfia* are solid, the internodes being filled with pith. In the larger plants of *Neostapfia*, the decumbent culms form a zig-zag pattern, thereby providing additional support of the plant's superstructure. Branching is basal in all of the grasses except *Orcuttia tenuis*, which is literally "top-heavy." A single, filiform, culm, often with adventitious roots from the lower nodes, supports the entire ramification above, and when excessively branched the whole plant becomes decumbent.

The mature inflorescences in both genera are exserted, except for *Orcuttia mucronata*, which is partially included. *Neostapfia* has a cylindrical, spike-like panicle, the terminal portion differing from the rest of the rachis in bearing small, closely appressed, lanceolate bracts. In *Orcuttia* the inflorescences are spikes or racemes, the shape varying among the species. The spikes of *Orcuttia pilosa* and *Orcuttia tenuis* are more or less elongated, with mostly distichous spikelets. A spiral arrangement of spikelets exists in *Orcuttia greenei* and *Orcuttia mucronata*, with the inflorescence somewhat elongate. In *Orcuttia californica* var. *inaequalis* and *Orcuttia californica* var. *viscida* the spike is sub-capitate, with a secund arrangement of spikelets.

The spikelets in *Neostapfia* are most unusual. They are without glumes, and the florets are so arranged as to suggest a trimerous cluster of spikelets. The florets are secund, the two lower ones divergent, the three or four upper ones closely imbricate. Disarticulation normally occurs between the florets, but occasionally below the spikelets, the rachis being continuous. In *Orcuttia* the spikelets are solitary, the floret number variable from 5-10 in *Orcuttia mucronata* to 10-30-, or even 40 in other species. Except for *Orcuttia tenuis*, there is little or no disarticulation of the florets, the whole inflorescence largely non-shattering. The culms of *Orcuttia greenei* are excessively fragile at the base, and the mature seed heads are readily deposited upon the surface of, or cracks in, the adobe soil.

The form of the lemma apex is an excellent diagnostic character for both genera. Along with the form of the inflorescence, it is employed consistently in identification keys and will not be discussed here. The lemma texture in *Neostapfia* is papery except for the tough nerves, while the *Orcuttia* lemmas are coriaceous.

Mature grains of both genera were examined from the material collected during 1958. In common they show: a loose enclosure between the lemma and palea, lateral flattening with the embryo extending along one side, a large basal hilum, persistent style base at the apex, and compound starch grains in the endosperm. The *Neostapfia* grains are obovate, completely viscid, and dark brown in color. Those of *Orcuttia* are oblong, not or scarcely viscid, and the embryo and hilum are conspicuously brownish in contrast to the light-colored endosperm.

Lodicules are apparently absent in all except *Orcuttia mucronata*, and here their unique appearance (fig. 3-D) suggests that a sectional division should be made to accommodate this species in *Orcuttia*; or possibly the lodicules along with other characters suggest that generic rank is merited.

The similarity of habitats, growth habit, and convergence of some morphological features indicate a rather close relationship between *Orcuttia* and *Neostapfia*, while their affinity to other grasses is not readily apparent. They should be removed from the Festuceae and might well be considered as a separate tribe.

VI. SUMMARY

1. *Orcuttia* and *Neostapfia* are restricted to a special type of vernal pool or "hog-wallow" which limits their geographic distribution. The association patterns of both *Orcuttia* and *Neostapfia* are truly remarkable and would constitute excellent material for detailed ecological studies. In certain areas, as revealed by the preceding account, *Neostapfia* occurs with only certain species of *Orcuttia* or stands alone. Likewise, only rarely are two species of *Orcuttia* associated, but if so, one of them is represented by only a few scattered individuals. All, however, demand the relatively large vernal pool beds for successful perpetuation.

2. It is suggested that their varying abundance from year to year is dependent upon the amount of rainfall and upon a long period of seed viability.

3. Morphological developments are a natural consequence of the environment with specializations directed towards viscidity, aroma, pubescence, and non-shattering inflorescences. Both genera are closely related, undoubtedly forming a natural grouping among the grasses, though their relationship to others is rather obscure.

4. A new species of *Orcuttia* from Solano County is described and illustrated.

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THE TAXONOMIC RELATIONSHIP BETWEEN PICEA
GLAUCA (MOENCH) VOSS AND P. ENGELMANNII PARRY¹

T. M. C. TAYLOR

For many years botanists and foresters have been puzzled and frustrated by the spruce complex in British Columbia, particularly the plexus centering around *Picea glauca* (Moench) Voss (White spruce) and *P. engelmannii* Parry (Engelmann's spruce). In the northern parts of the province *P. glauca* appears in its typical form and is a clear-cut entity. At higher altitudes in the southern interior of the province *P. engelmannii* may be found in equally characteristic form. Unfortunately, between these two easily distinguishable extremes there is a great range of intermediates. The taxonomic, and hence the nomenclatural, disposition of these intermediates is the substance of the present paper.

Materials studied were collected largely at Banff, in the Upper Columbia Valley, and in the Cranbrook-Moyie Lake area. This southeastern region of the province and adjacent Alberta was selected because here the problem raised by the intermediate forms of spruce is particularly acute. Collections were made with the primary purpose of gaining a statistical picture of the variability between individual trees of certain mensural characters of leaves and cones. It was felt that only when the extent of variation within the individual was established, could one proceed with confidence to generalizing from small samples drawn from many trees.

Materials were collected from about seventy randomly selected trees. In case the degree of shading might produce constant differences, cones and twigs with needles were taken from both the north and south side of trees. Needles were also collected from both vegetative and reproductive shoots. Statistical analysis showed no significant difference between samples from the north and south side, nor between needles from reproductive and vegetative twigs. In the present report therefore this distinction is not maintained.

The difficulty of making accurate measurements of curved leaves was overcome by boiling them for five minutes to render them pliable so that they could be straightened out. Spreading of the scales in dry cones also offered complications for measurement but these complications were also overcome by boiling the cones until they sank. By this time the scales had contracted and were closely appressed in the cone. It was established that prolonged boiling produced no further change in dimensions.

Mention may be made of the findings on intra-tree variability. Needle lengths, with means of the order of 13.5 mm. and standard deviations of about 2 mm. showed coefficients of variability ranging from about 11 to 20. Cone diameters with means of the order of 13.5 mm. have standard deviations of slightly over 1 mm. with a range in the coefficients of vari-

¹ This study was supported in considerable measure by financial assistance from the National Research Council of Canada to which body grateful acknowledgment is made.

ability from 6 to 10. Cone lengths were about 42 mm., with standard deviations about 3.5 mm. and variability with coefficients about the same as for diameters.

One can conclude then that needle lengths are very variable on the same tree and that a large number would have to be measured in order to obtain a statistically satisfactory mean value. Cones, on the other hand, are much more uniform in dimensions and so smaller samples per tree would be acceptable.

The most obvious difference between Engelmann's and White spruce is in the cone scale. Those of the former are thin and somewhat papery, wedge-shaped with wavy to erose margins, and commonly erose to truncate at the apex. The scales of the White spruce on the other hand, are obovate-triangular, somewhat stiff with entire margins, the apex being rounded or somewhat flattened, not erose. It was possible to interpolate three classes of intermediates between these extremes. In the accompanying tables the five cone type classes are numbered in Roman numerals with *P. engelmannii* I and *P. glauca* V. Table 1 shows the means and standard deviations of cone diameters and lengths for the five cone type classes. The differences between the means of diameter are not reliable while the differences in mean length of types I and V is reliable at the level of .01. The erratic means of length for types in II, III and IV are presumably due to inadequacy of the samples. This, however, is a matter that requires further investigation.

TABLE 1. Relationship between cone dimensions and cone type in *Picea engelmannii*, *P. glauca*, and intermediates.*

Cone type	Diameter				Length			
	M	SD	N	n	M	SD	N	n
I	13.7	1.13	14	521	45.0	3.11	14	518
II	14.0	1.12	12	349	46.1	6.57	11	328
III	13.4	1.03	6	207	41.8	3.72	6	199
IV	13.6	1.28	6	368	43.1	3.00	6	377
V	13.4	1.27	21	1449	41.4	3.96	21	1491

* I represents *P. engelmannii*, V, "P. glauca," II-IV, intermediates. M = mean (in mm.), SD = standard deviation (in mm.), N = number of trees sampled, n = number of cones measured.

Analysis of needle length showed no significant differences between the means for the different cone types. Engelmann spruce needles, however, tended to be straight and slender, acuminate and somewhat square in cross-section, while those of White spruce were firmer, often curved and rounded at the apex, tending to be dorsiventrally flattened or triangular in section. Needles with these characteristics in other combinations were classed as "intermediates." Table 2 shows the relationship found between leaf type and cone type. It is apparent that foliage characters are not correlated with cone types and are probably due to the independent segregation of several genes.

TABLE 2. Relationship between leaf type and cone type in *Picea engelmannii*, *P. glauca*, and intermediates.*

Leaf types	Cone types					
	I	II	III	IV	V	N
'engelmannii'	9	7	5	21
intermediate	12	4	4	7	8	35
'glauca'	1	13	14
Totals	21	11	9	8	21	70

* I represents *P. engelmannii*, V, *P. glauca*, II-IV, intermediates. N = number of trees sampled.

The relationship between the indumentum of the twigs and cone types was also studied. Twigs of White spruce are characteristically glabrous, while those of Engelmann's spruce have a short, crisp pubescence. In Table 3 it can be seen that all cone types may be borne on trees with pubescent twigs, except that cone type V has an equal chance of being borne on a tree with glabrous twigs. One can speculate that the development of indumentum is controlled by a single pair of genes and that "pubescence" is dominant.

TABLE 3. Relationship between indumentum of twigs and cone in *Picea engelmannii*, *P. glauca*, and intermediates.*

Twigs	Cone types					
	I	II	III	IV	V	N
Pubescent	21	10	9	8	11	59
Glabrous	1	10	11
Totals	21	11	9	8	21	70

* I represents *P. engelmannii*-type, V, *P. glauca*-type, II-IV, intermediates. N = number of trees sampled.

It is apparent that White and Engelmann's spruce are very much alike and that even such diagnostic features as mean cone length, and shape and character of the scales are merely the extremes of a series of intermediates. Both 'engelmannii' and 'glauca' needle types are found on trees with 'intermediate' type cones and 'intermediate' type needles may be associated with any type of cone. Glabrous twigs have only been found on trees with 'glauca' cones but, on the other hand, there is an equal chance that the twigs on such trees will be pubescent. On several occasions in the past it has been commercially important to try to distinguish lumber cut from these two spruces. No differentiating histological details have been found and Barton and Gardner (1957), using partition chromatography in addition to infra-red and ultra-violet spectrographic methods, failed to establish any chemical differences between the woods.

Wright (1955) has examined in considerable detail the question of interspecific hybrids in *Picea*. In his paper he attempts "to correlate species

crossability with geographic distribution, morphology, and phylogeny." He examined thirty-one species with respect to fifty-one characters that show differences between some or other of these species. The majority of the characters, of course, do not lend themselves to measurement and are to quite an extent subjective. It is regrettable that Wright's observations were not analyzed statistically. Had they been, the relationship between *P. glauca* and *P. engelmannii* would likely have appeared very much closer than he concludes.

Wright (1. c.) has made some investigation of hybridizing between White and Engelmann spruce. Using a hybridity index, he shows that very considerable introgression is taking place over a wide area extending from latitude 51° to 58° N. and between longitude 109° to 124° W. That these intermediates are almost certainly of hybrid origin is borne out by his report of successful reciprocal crosses between the two species.

Garman (1957) has made a detailed morphological and distributional study of spruce populations in British Columbia. Using a "morphological index" on which pure *P. glauca* rates 6 and pure *P. engelmannii* rates 18, he shows the very extensive geographic area occupied by intermediates on this scale. This index has apparently proven useful in distinguishing populations, but its value would be greatly enhanced if the measurable characters had been treated statistically. Only average values and ranges of measurement are given and, as the latter frequently overlap, their significance cannot be evaluated.

In the opinion of the present author, the phylogenetic relationship between *P. glauca* and *P. engelmannii* is best indicated by regarding them as subspecies of a single species and so the following changes in status are proposed. According to the provisions of Article 57 of the International Code of Botanical Nomenclature (Lanjouw 1956) *Picea glauca* (Moench) Voss, which has priority, becomes the legitimate name when the two species are combined into one.

PICEA GLAUCA (Moench) Voss subsp. *glauca*

Abies canadensis Mill. Gard. Dict. Ed. 8, Abies No. 4, 1768; *nomen confusum*
Pinus glauca Moench, Verzeichn. Baeume Weissenst. 73. 1785
Pinus alba Ait. Hort. Kew. 3:371. 1789
Picea laxa Sargent, Gard. and For. 2:496. 1889
Picea glauca (Moench) Voss, Mitt. Deutsch. Dendr. Ges. 1907:93. 1907
Picea glauca var. *porsildii* Raup, Sargentia 6:102. 1947

PICEA GLAUCA (Moench) Voss subsp. *engelmannii* (Parry) stat. nov.

Abies engelmanni Parry, Trans. Acad. St. Louis 2:122. 1863; *nomen nudum*
Picea engelmanni Parry ex Engelmann; Trans. Acad. St. Louis 2:212. 1863
Picea columbiana Lemmon, Gard. and For. 10:183. 1897

There is little doubt that *Picea glauca* var. *albertiana* (S. Brown) Sargent (*Picea albertiana* S. Brown, Torreya 7:126. 1907) is based on an individual of the hybrid swarm between subsp. *glauca* and subsp. *engelmannii* and in consequence this name should no longer be perpetuated. When reference is made to these hybrid intermediates it should be done

by employing a formula as provided by Article H.2 of the International Code with particular attention to the "Note."

Goodman (1950), in describing his *P. engelmannii* var. *glabra*, almost certainly had at hand a biotype of Engelmann's spruce that showed the result of the introgression of genes from the glabrous White spruce.

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FIELD STUDIES OF NATURAL HYBRIDIZATION IN THE OREGON SPECIES OF IRIS L. SUBSECTION CALIFORNICAE DIELS

QUENTIN D. CLARKSON

Smith and Clarkson (1956) have discussed the cytological aspects of hybridization in *Iris*, subsection *Californicae*. They reported that, with the exception of *I. tenuis* Wats., which has been removed to a new subsection (Clarkson, 1958), all the members of the subsection studied had a uniform chromosome morphology, and all contained a diploid number of forty. Fertile hybrids were produced experimentally without difficulty and all were highly fertile except that hybrids involving *I. tenuis* as a parent could not be produced. This paper will discuss some natural hybrids of those taxa occurring in western Oregon and will propose certain nomenclatural revisions. Because the subsection was treated taxonomically by Foster (1937), conventional citations will not be included except for taxa described since that time.

DISTINGUISHING CHARACTERISTICS. Aside from the usual characteristics of the genus *Iris*, the members of the subsection *Californicae* are distinguished by a usually deltoid stigma; D-shaped, cubical or ovoid seeds; the absence of foliaceous stem leaves; and tough basal leaves which are reddish at base. A number of characteristics have been used for distin-

guishing species by various authors, including Foster (1937) and Dykes (1912) in the two most complete reviews of the subsection. These have been evaluated with herbarium specimens (Clarkson, 1950) and with living material. Those characters which allow ready distinction of taxa and which are most easily utilized for study of hybrids are as follows:

Perianth. The petals are usually narrow and about the same length as the sepals which are linear to spathulate in shape. Color of the perianth ranges from white, purple, pale yellow, golden yellow, to apricot and maroon.

Perianth tube and pedicel. The perianth tube varies in length from 0.4 to 12 centimeters with the pedicel varying approximately inversely.

Bracts of the inflorescence. The bracts, or spathes, are variable in shape from ovoid to linear; in length from 2 to 15 centimeters; and in position from opposite to alternate.

FIELD STUDIES. Although a quantitative study of morphological and ecological characteristics was desirable, inadequate knowledge of distribution of the species and the absence of definite knowledge of natural hybrids made such work impossible. Field work was therefore conducted on a qualitative basis. A limited number of transplants made during current field work and previously by Smith (Smith and Clarkson, 1956) demonstrate that the characteristics of the taxa are constant under varying environmental conditions. Herbarium specimens designed to represent all the variation present in a given location were collected. These mass collections are in the possession of the author.

Results of field studies are given below together with interpretations of their significance.

HYBRIDS BETWEEN *I. TENAX* AND *I. CHRYSOPHYLLA*

Iris tenax is characterized by narrow, distant bracts; a perianth tube from 4 to 9 millimeters in length and by lavender to purple flowers with broad spathulate sepals. The plants are tall and with definite stems. Though the species is typically purple-flowered, two yellow-flowered populations have been found. One of these is along Scoggins Creek in Washington County, Oregon. It has been treated as *I. gormanii* Piper and more recently as *I. tenax* var. *gormanii* (Piper) Foster. The second yellow-flowered population is on Monument Peak, Linn County, Oregon. This local population is apparently not well known and has not been cited in the literature of the subsection. Neither of these populations can be distinguished from the typical phase of *I. tenax* by any trait other than color.

The general range of the species is from the central part of western Washington to southern Oregon. Ecologically it is a species of unshaded conditions and is abundant on the oak-covered hills of the Willamette and Umpqua valleys. It does not extend into coniferous areas unless trees are cut, roads built, or conditions otherwise disturbed in such a way that shading is reduced. Within the general range there seem to be no soil or moisture factors limiting its distribution. Factors controlling the northern and southern limits of the species range are probably climatic in nature.

Iris chrysophylla is characterized by lanceolate, opposite bracts; a perianth tube 5 to 9 (occasionally to 12) centimeters in length; a pedicel less than 1 centimeter in length; and by pale yellow flowers with narrow perianth parts. In southwestern Oregon, where the species is most abundant, well-marked stems are produced. In the Cascade Mountains of northern Oregon, the plants are often nearly stemless. Plants at two previously unreported stations of the species, Mill Creek, Polk County, Oregon, and Prairie Mountain, Benton County, Oregon, are of the Cascade type.

Ecologically *I. chrysophylla* is a species of open coniferous forests. It grows best on drier soils and will tolerate more shade than *I. tenax*. It is a characteristic species of the ponderosa pine and ponderosa pine-Douglas fir communities of southwestern Oregon.

Distinctive hybrids between *I. tenax* and *I. chrysophylla* have been found in three locations: (1) 4½ miles up Mill Creek from the Dallas—Wallace Bridge highway, Polk County, Oregon; (2) 13¼ miles southwest of Roseburg, Douglas County, Oregon, along Oregon State highway number 42; (3) steep hills along the first tributary of the North Santiam River west of the Detroit Dam, Marion County, Oregon. In all three locations conditions have been disturbed by road construction.

At all three of these sites individuals have been found which are intermediate between the parent species and which cannot be assigned to either species. Bracts of the hybrids are opposite and are broader than is characteristic of *I. tenax* but not so broad as those of *I. chrysophylla*; flower color is maroon to grayish-lavender; and the perianth parts are slender. The plants are smaller than typical *I. tenax* but have a definite stem. Perianth tube length in the natural hybrids averages 2.2 centimeters and the pedicel averages 1.4 centimeters. Comparative measurements in the known hybrids are perianth tube 2.5 and pedicel 1.8. This indicates that the hybrids are possibly of the *F*₁ generation. In other characters the natural hybrids compare closely with the known hybrids.

The area of overlapping ranges is, in all three cases, small. At Mill Creek and along the North Santiam highway, a transect of less than 100 yards extends through the area occupied by both species. At the site southwest of Roseburg, a similar transect extends less than one-half mile.

Hybrids between these two species appear to be introgressive toward *I. tenax*. Individuals identifiable as *I. tenax* show definite *I. chrysophylla* characteristics for at least ten miles from the area where typical *I. chrysophylla* occurs. These individuals exhibit a change in color toward a pale purple; a reduction in size; and a tendency toward broader and less distant bracts. These modifications in *I. tenax* are what might be expected as a result of hybridization with *I. chrysophylla*. The intermediates previously discussed are found in the areas where the two species occur together but *I. chrysophylla* remains constant and no individuals of that species have been found which exhibit *I. tenax* characteristics.

Introgressive hybridization between these two species is a close parallel

of a situation described by Anderson (1949) in which hybridization is followed by backcrossing and selection of backcross types. Apparently, in this case, only the offspring of the intermediate \times *I. tenax* backcross are selected. The factors of the ecology which bring about this selection are not known. The introgression, however, has resulted in a considerable increase in the variability of *I. tenax* while *I. chrysophylla* has remained constant.

The occurrence of *I. chrysophylla* at two locations in the Coast Range of Oregon was not unexpected. The presence of individuals of *I. tenax* with lanceolate, opposite bracts in the Coast Range west of Corvallis, Oregon, suggested possible hybridization with *I. chrysophylla*. At the Mill Creek location in Polk County, Oregon, the two species are in contact at the present time, as was previously mentioned. At Prairie Mountain, Benton County, Oregon, there is no present day contact on the north and probably not on the south. *Iris chrysophylla* is abundant on a broad, well-drained meadow, along a south-facing slope near the summit of Prairie Mountain at an elevation of about 3200 feet. *Iris tenax* is not now in contact on the north, presumably because of the dense growth of Douglas fir on that side. The south side of the mountain is more open and the two species may come together though no intermediates have been found. *Iris tenax* specimens collected at Horton, Lane County, eight miles to the south, have a narrower and more pale perianth which suggests hybridization with *I. chrysophylla*.

Thirty miles north of Prairie Mountain are individuals of *I. tenax* with linear-lanceolate, opposite bracts, and narrow, pale purple perianth parts. These plants are probably the result of introgression from *I. chrysophylla* to *I. tenax*. These hybrid forms indicate either that *I. chrysophylla* is more abundant in the Coast Range than is now known or that it was more abundant in the past and has survived only on the more favorable sites. Either hypothesis may be true in part, but it seems unlikely that these forms are the result of recent hybridization. *Iris chrysophylla* has not been found in the Coast Range between Prairie Mountain and Mill Creek, and distances are probably too great for plants at those locations to be involved as parents. The most probable explanation is that *I. chrysophylla* was more abundant in the Coast Range of northern Oregon in the past and has remained only at the dry, open sites such as Mill Creek and Prairie Mountain. The occurrence of a warm, dry period in postglacial times, followed by general cooling and increase in moisture (Hansen, 1947) makes this a reasonable assumption. Whether *I. chrysophylla* was distributed throughout the general area of northwestern Oregon in the past or only on the higher peaks, is a question which cannot be answered. In either case, abundant opportunities for hybridization could have existed. Introgression, such as occurs today, could have given greater adaptive value to *I. tenax* while *I. chrysophylla* remained more nearly constant and more vulnerable to environment change.

There is, however, no reason to suppose that the yellow-flowered forms

of *I. tenax* on Monument Peak and in Washington County, Oregon, are of hybrid origin. All the hybrids between these two species, including the artificial hybrids produced for this study, exhibit a tendency toward the lanceolate, opposite bracts of *I. chrysophylla*. The purple flower color is reduced to greyish-lavender in the known F_1 hybrids, and none of the hybrids found in nature have yellow flowers. An independent origin for this color trait is not improbable as evidenced by *I. hartwegii*, which is closely related to *I. tenax* and has yellow flowers and by the fact that there are yellow-flowered forms in *I. macrosiphon* which is otherwise purple-flowered.

HYBRIDS BETWEEN *I. DOUGLASIANA* AND *I. INNOMINATA*

Iris douglasiana is a tall species averaging about 60 centimeters in height and is characterized by leaves about a centimeter wide; a branching stem; lanceolate, opposite bracts; large pale purple to white flowers; and a perianth tube 1 to 2 centimeters in length. Two or three flowers per branch are produced. Distribution of the species in Oregon is limited chiefly to a narrow, open coastal strip from Coquille, Coos County, southward. The species normally extends inland only along river valleys. It has not been seen in dense shade.

Iris innominata is a low species averaging about 35 centimeters in height and is characterized by narrow leaves which are about 4 centimeters wide; simple stems; ovate, opposite bracts; small, golden yellow flowers; and a perianth tube 1 to 2.5 centimeters in length. Distribution of the species is limited to the open meadows and hills of southern Douglas, Coos, and Curry counties, Oregon.

Hybrid colonies of about 100 plants each of the *I. douglasiana* \times *I. innominata* cross have been found along Saunderson's Creek, Curry County, Oregon. The two sites are 1½ and 2½ miles from the Rogue River, 3 miles upriver from Gold Beach on the south side of the Rogue River. The colonies are found in cut-over forest land with most of the plants completely exposed to the sun, though a few are found in the shade of *Umbellularia californica*. Some of the individuals are similar to the known hybrids grown for cytological study. Perianth size and plant size appear to be intermediate between the parent species and the bracts are shorter and more ovoid than are those of *I. douglasiana* but are longer and narrower than those of *I. innominata*. These individuals may be F_1 hybrids. Other plants appear to be the result of backcrossing and segregation.

Aside from the demonstration of genetic continuity between species, the taxonomic significance of the hybrids is considerable. Some individuals from one of the hybrid colonies compare closely with individuals referred to *I. thompsonii* Foster. There is a strong suggestion of the hybrid origin of that taxon. *Iris thompsonii* has been collected along the Rogue River and along United States Highway 101 from Carpenterville to Brookings, Curry County, Oregon. In California, it has been collected along the Smith River, northeast of Crescent City, Del Norte County. The

species can be distinguished from *I. innominata* by the more lanceolate bracts and by the pale purple to lavender flower color. It also seems to be taller, averaging about 45 centimeters. These are characteristics which could be fixed by backcrossing of the *I. douglasiana* \times *I. innominata* hybrids to *I. innominata*.

A similar hypothesis can be erected to explain those specimens with more ovate bracts and lavender-grey flowers referred by Foster (1937) to a new variety, *I. douglasiana* var. *oregonensis*. Backcrossing of the intermediates of the *I. douglasiana* \times *I. innominata* cross to *I. douglasiana* could result in the fixing of these *I. innominata* traits in otherwise typical *I. douglasiana*.

While both assumptions are largely hypothetical, they are lent support by the occurrence of these variants in an area where the two species come together and hybridize. The only barriers seem to be ecological, though exact factors cannot be stated. The removal of the forest trees with the accompanying reduction in shade has apparently removed the barrier to hybridization in the case discussed here, but elevation and soil factors may be important in other locations. However, hybrids probably will be found wherever the hills of Coos and Curry counties are near the ocean and conditions are disturbed or where *I. douglasiana* extends inland along river valleys. In these areas, at least, the two species can be expected to occur together.

HYBRIDS BETWEEN *I. BRACTEATA* AND *I. THOMPSONII*

Iris bracteata is a tall species averaging about 50 centimeters in height and with a thick perianth tube 0.5 to 1.0 centimeter in length, a pedicel 3 to 6 centimeters long, and golden yellow flowers. Typically the leaves are a glossy green on the upper surface and glaucous on the lower. The species has been seen only in southwestern Josephine County, Oregon, and northeastern Del Norte County, California. Ecologically it is restricted to shaded places. The species is found in greatest abundance within ponderosa pine communities, but it is sometimes found on cut-over forest land under a cover of bracken fern.

Iris thompsonii has been discussed as a possible hybrid segregate of the *I. douglasiana* \times *I. innominata* cross. Colonies are best developed along the lower Smith River, from 12 to 15 miles northeast of Crescent City, California. In this location, the colonies are well established on open rocky hillsides, and have not been seen in the shade.

Proceeding northeastward from Jedediah Smith State Park in Del Norte County, over the Siskiyou Mountains into Oregon, the colonies become more shade tolerant. Color changes gradually from predominantly pale purple flowers to predominantly yellow flowers, though a few white-flowered plants are present. Bract characteristics appear to be intermediate between the two species, changing gradually from ovoid and 5 centimeters long, to narrower and 7 centimeters long. Height of the plant also becomes progressively greater as colonies nearer typical *I. bracteata* are

examined. Three miles north of the summit of the Siskiyou Mountains only typical *I. bracteata* has been seen.

No individuals similar to the known F_1 hybrids have been found in nature. The transition between the two species is gradual, probably because of ecological requirements which permit more hybridization and survival of most of the hybrid offspring.

HYBRIDS BETWEEN *I. BRACTEATA* AND *I. CHRYSOPHYLLA*

Distinct hybrids between these two species have not yet been clearly demonstrated. Despite the pronounced morphological differences between the two, only one individual has been secured which can be considered intermediate. The relationship of the perianth tube to the pedicel is reversed in these two species. *Iris chrysophylla* has a perianth tube 5 to 6 times longer than the pedicel. In *I. bracteata* the pedicel is 5 to 6 times longer than the perianth tube. In the intermediate specimen cited above, the pedicel is twice the length of the perianth tube, clearly not characteristic of either *I. chrysophylla* or *I. bracteata*. This specimen was collected near Bridgeview, Josephine County, Oregon, where the two species occupy the same general area.

Complementing this admittedly limited evidence, field examination reveals hybrid characteristics which are not readily demonstrable with pressed specimens. Near Cave Junction, Josephine County, there are individuals of *I. bracteata* with narrow perianth segments characteristic of *I. chrysophylla*. The hybrid origin of these individuals is supported by the fact that all the known hybrids involving *I. chrysophylla* as a parent exhibit the narrow perianth of that species. There are also individuals, in the Cave Junction area, of *I. chrysophylla* with perianth color similar to the golden yellow of *I. bracteata*. The known *I. bracteata* \times *I. chrysophylla* hybrid has golden-yellow flowers and all other crosses involving golden-yellow and pale yellow-flowered parents show the flower color of the golden-yellow parent.

TAXONOMY. Due to the absence of cytological barriers between taxa and the presence of natural hybrids, nomenclatural revision which will better reflect the biology of the organisms seems necessary. Therefore, the following new combinations are proposed. Further field work is needed before accurate limits can be set for the California members of the subsection and they will not be considered here.

1. **IRIS TENAX** Dougl. subsp. **TENAX** (*I. tenax* Douglas ex Lindley, Bot. Reg. xv. t. 1218, 1829). This subspecies includes the typical form which has been discussed previously in this paper as *I. tenax*. Also included, without nomenclatural distinction, is the yellow-flowered *I. tenax* var. *gormanii*. The yellow-flowered form from Monument Peak, Linn County, Oregon, will be included within *I. tenax gormanii* and therefore within *I. tenax tenax* without nomenclatural distinction.

2. **IRIS TENAX** subsp. **CHRYSOPHYLLA** (Howell) (*I. chrysophylla* Howell, Fl. N. W. America 1:633, 1902). No type specimen was designated

for Howell's *I. chrysophylla*. However, filed with the type specimen collection at the herbarium of the University of Oregon is a specimen labeled "Type specimen" in the distinctive handwriting of Thomas Howell. This specimen, collected at Grants Pass, Josephine County, Oregon, in May 1887, must be considered the type specimen for Howell's species and therefore for the proposed subspecies.

3. *IRIS TENAX* subsp. *BRACTEATA* (Watson) (*I. bracteata* Watson, Proc. Amer. Acad. 20:375, 1885). This subspecies includes the species as described by Watson.

4. *IRIS TENAX* subsp. *DOUGLASIANA* (Herbert) (*I. douglasiana* Herbert, Bot. Beechey Voy. 395, 1841). Included in *I. tenax douglasiana* without nomenclatural distinction is *I. douglasiana* var. *oregonensis* Foster. So long as it is understood that Foster's variety is probably of hybrid origin, there is no need to distinguish a form which obviously belongs to what has been described as *I. douglasiana*. Since this subspecies is found in California as well as Oregon, this new combination must necessarily include the California plants. This does not mean that the California plants of this taxon should be ignored in any further study. There is undoubtedly considerable variation present that is not included in the Oregon representatives.

5. *IRIS TENAX* subsp. *INNOMINATA* (Henderson) (*I. innominata* Henderson, Rhodora 32:23, 1930). This subspecies has been retained as originally described except for the reduction in rank.

6. *IRIS TENAX* subsp. *THOMPSONII* (Foster) (*I. thompsonii* Foster, Rhodora 38:199, 1936). The only real difference between this proposed new subspecies and *I. tenax innominata* is in the purple flower color of *I. tenax thompsonii*. Since it has been suggested that *I. tenax thompsonii* may be of hybrid origin with *I. tenax innominata* as one parent, a close morphological relationship is to be expected. The two taxa differ slightly in distribution, *I. tenax thompsonii* is a species of elevations between 400 and 1000 feet while *I. tenax innominata* is usually at sites over 1500 feet. For that reason and because *I. tenax thompsonii* does form distinct colonies, it is retained.

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VARIATION PATTERNS IN FOUR CLONES OF
MERTENSIA CILIATA¹

JEANETTE S. PELTON

Mertensia ciliata (James) G. Don is well delineated from other species of the genus in the monograph by Williams (1937). Field observations in the area of the present study, Gunnison County, Colorado, bear out this distinctness of *M. ciliata* from other sympatric species, although considerable intraspecific variation is easily detected. In spite of the fact that certain other species of the group grow sympatrically in the study area with *M. ciliata*, five years of observation by the author have not uncovered a single likely instance of hybridization between *M. ciliata* and any of the other species. Nor did artificial cross pollination produce any fertile seed between *M. ciliata* and *M. fusiformis* Greene. In the observed populations, therefore, *M. ciliata* seems an excellent species in which to study quantitatively intraspecific variation patterns which are probably uncomplicated by any present inflow of genes from another species. With this objective in mind, three floral characteristics within and among four clones of *M. ciliata* were chosen for study. The clones were selected such that each was separated from the other by a distance of one-third to two miles. Such a distance probably assures that each clump is an individual clone with a different genetic origin. Hence the four clumps will be referred to hereafter as clones A, B, C, and D. Since each clone was growing in a different combination of environmental factors, at least four of the many micro-habitats to which individuals of *M. ciliata* are adapted are represented. By selecting clones in the above manner, it was presumed that a measure of somatic variability could be obtained, since the phenotypic measurements would be made upon single genotypes each produced in a slightly different environment. In addition, differences in gene expression among the clones imply possible genetic variation patterns.

METHODS AND RESULTS

Clones A, B, C, and D were collected in the summer of 1953 in or near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. No clone was nearer than approximately one-third mile from another, and all clones were located on different drainage channels. The altitude is approximately 9,500 feet for three of the clones and 10,000 feet for Clone B. Voucher specimens of the collections are in the personal herbarium of the author.

Length of calyx, corolla-tube, and corolla-limb were measured from these herbarium voucher specimens. In this study the corolla-limb, as defined by Williams (1937), will include that portion of the corolla above the fornices. Individual mature flowers were measured for the three floral characteristics to 0.5 mm. using low power of a binocular microscope to

¹ The author is grateful for the use of facilities of the Rocky Mountain Biological Laboratory and to Dr. John F. Pelton for criticisms and additions to the manuscript.

TABLE 1. Arithmetic mean, standard deviation, and range of variation for length of calyx, corolla-tube, and corolla-limb in four clones of *Mertensia ciliata*

Clone	No. of Individuals	Calyx Length			Corolla Tube Length			Corolla Limb Length		
		Mean	Standard Deviation	Range of Variation	Mean	Standard Deviation	Range of Variation	Mean	Standard Deviation	Range of Variation
A	150	2.5	0.24	2.0-3.5	5.4	0.52	3.5-6.5	5.9	0.70	4.5-8.0
B	94	1.8	0.30	1.5-2.5	6.2	1.51	5.0-7.5	7.3	1.04	5.0-9.5
C	132	1.8	0.33	1.5-2.5	6.8	0.50	5.5-8.0	6.1	0.88	4.0-8.0
D	40	2.1	0.30	1.5-2.5	5.9	0.36	5.0-6.5	7.1	0.79	5.0-9.0

increase accuracy. Arithmetic mean, standard deviation, and range of variation were determined for each characteristic measured in the four clones. These results are presented in Table 1. In Figure 1 variation among the four clones is diagrammed using mean length of calyx, corolla-tube and corolla-limb. Range of variation within the clones is diagrammed in Figure 2.

Descriptions of the clones are as follows:

CLONE A. Collected July 15 from a moist roadside site one-fourth mile north of the laboratory. The clump was growing on the edge of a dense willow thicket in full sun. There was a total of 14 individual stems in the clone, averaging 10.7 mature flowers per stem. Total number of mature flowers measured was 150.

CLONE B. Growing in a very wet location in the partial shade of a spruce-fir forest on the edge of a beaver pond about two miles northeast of the laboratory at 10,000 feet and collected on July 19. The average number of mature flowers was 3.1 on a total of 30 individual stems; 94 mature flowers were measured.

CLONE C. Chosen from a population in an aspen forest on laboratory property. The clone was collected on July 23 in a partially shaded rocky stream bed. This clone had 32 stems, the largest number of individual stems of the four clones. Average number of mature flowers per stem was 4.1; 132 mature flowers were measured from this clone.

CLONE D. Growing in a willow thicket near Copper Creek adjacent to the laboratory. The soil was wet and rocky, the clone growing in partial shade. Collection was on July 7. The three individual stems of this clone, all flowering, averaged 13.3 mature flowers per stem and totaled 40 mature flowers suitable for measurement.

DISCUSSION

The variation pattern for each of the four studied clones of *Mertensia ciliata* is striking enough that a given clump can be identified on the basis of a distinctive combination of average length of calyx, corolla-tube and corolla-limb (fig. 1). On the other hand, individual measurements within

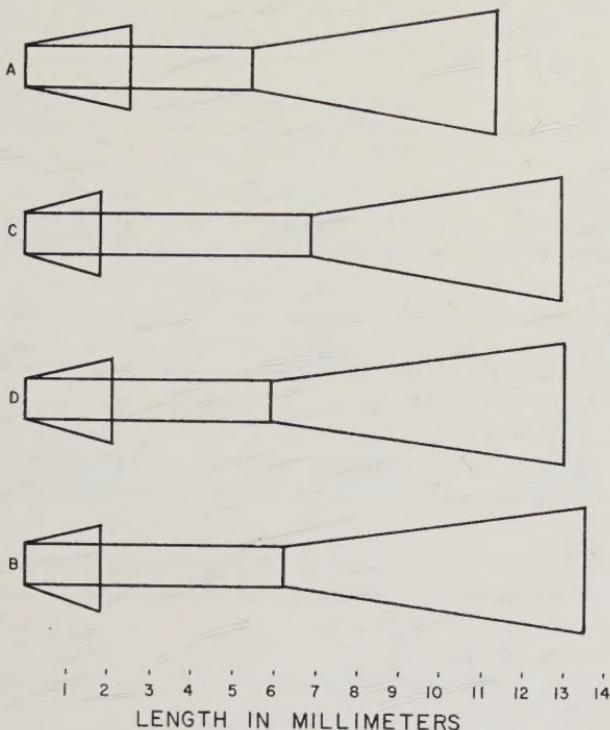


FIG. 1. Idiograms showing average lengths in millimeters of calyx, corolla tube, and corolla limb in clones A, B, C, and D of *Mertensia ciliata*.

each clone vary considerably for these three characteristics (fig. 2). However, the range of variation of a character in a clone usually does not overlap completely with that of the same character in other clones. These observed variations within and among the clones could be the result of three factors mentioned by Stebbins (1950): environmental modification, gene recombination, and mutation of genes or chromosomes. Considerations of the role of these factors as possible explanations for the variability observed is discussed in the following.

ENVIRONMENTAL MODIFICATIONS. Variability within a given clump should be a measure of environmental influences except for rare bud mutations or the unlikely possibility that one clump was derived from two or more seedlings. Floral characteristics were chosen for study because they are known to be frequently less easily influenced by environmental factors than are many vegetative characteristics (Clausen, Keck, and Hiesey, 1940; Anderson, 1929; Brainerd and Peitersen, 1920). All three characteristics vary considerably in range of measurements within each clone, such as the 1.5 mm. variation in Clone A calyx length which averages only 2.5 mm., the 3 mm. variation in corolla tube length in Clone

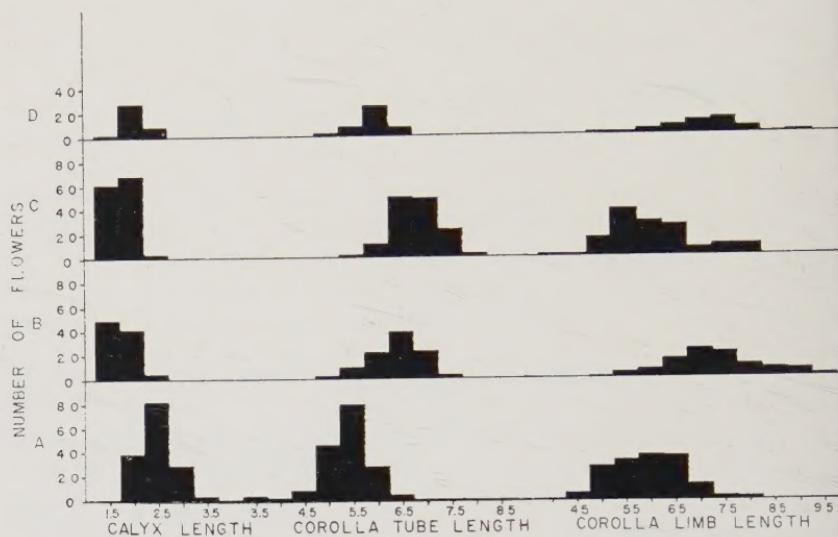


FIG. 2. Histograms showing distribution of individual measurements in millimeters of length of calyx, corolla tube, and corolla limb in clones A, B, C, and D of *Mertensia ciliata*.

A which averages 5.4 mm. in length, or the 4.5 mm. variation in corolla limb length for Clone B while average length is only 7.3 mm. This indicates that gene action, even in the fairly uniform environment of a single clone, differs in the final expression of length of calyx and corolla. To determine the various environmental factors that control the diverse action of these genes is difficult even in the imagination. External conditions such as soil, temperature, light, humidity, and biotic interactions would usually be expected to vary comparatively slightly during the development of the flower primordia of a single clump. Internal conditions such as amount and distance of the vascular supply, internal temperature, chemical environment, and the differing interaction of other genes in ontogeny would perhaps be more important than external environment since a slight variation of internal environment during the delicate interactions between gene initiation and the end result of expression could alter the phenotype. Whichever of the external or internal conditions may be important, their effect on the genes controlling calyx and corolla length accounts for a large proportion of the variation observed in this study, probably all of the intraclonal variability. This would support the idea that corolla and calyx length in this case are quantitative characteristics, dependent on multiple genes, since quantitative characteristics are usually subject to considerable modification by environment (Srb and Owen, 1952).

GENE RECOMBINATION AND MUTATION. While the somatic variation discussed above cannot result in permanent changes in the species, gene

recombination and/or gene and chromosomal mutation are thought to contribute to variation that can foster evolutional change in the species (Stebbins, 1950). Whether gene recombination and mutations could account for the differences among these four clones cannot be determined from the results of this study. Probably some of the observed differences among clones would be attributed to dissimilarities in external or internal environments of the four clones. It must be noted again, however, that floral characteristics are probably less subject to environmental modification than are other features of external morphology. Floral differences based on the pattern of average length of calyx, corolla-tube, and corolla-limb illustrate a distinctive combination in each clone (fig. 1). On close examination of the individuals compounded in these means it is found that only a few flowers approach the extremes of the large range of variation, and that standard deviations, given in Table I, are not large. Also, the histograms for each clone do not closely coincide with those for the other clones, although considerable overlapping does occur (fig. 2). These patterns of difference among the clones are probably the result of gene recombination, mutation because of its rarer occurrence being a less likely source. If *Mertensia ciliata* has a large number of genes active in regulating corolla length, such as the estimated twelve or more controlling corolla size in *Nicotiana* (Smith, 1937), it would be plausible to assume such recombination of the many genes in different individual plants or clones. Close linkage between the polygenes that determine quantitative characteristics, however, is often assumed to restrict the range of recombination of characteristics (Smith, 1944). Nevertheless, while somatic variation is doubtless the main factor in accounting for the variation within each clump, the characteristic variation patterns presented here for calyx and corolla length would imply some genetic differences among the clones, probably, as a result of gene recombination.

SUMMARY

Length of calyx, corolla-tube, and corolla-limb were measured for four widely separated clumps, presumably clones, of *Mertensia ciliata* that were collected from four differing and widely separated sites in Gunnison County, Colorado. Comparisons of calyx and corolla lengths were made within and among the four clones. The considerable variation of the three characteristics found within each of the clones is attributed to external and internal environmental factors, internal conditions probably being more important. Variation patterns among the clones differ enough to give each clone a distinctive combination of average lengths for the three characteristics. In most cases, the range of variation in calyx and corolla length within each clone does not completely coincide with that of the other clones. These differences in variation patterns imply some genetic differences among the clones, probably as a result of gene recombination.

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NEW COMBINATIONS IN ASTER

ROXANA S. FERRIS

Through an inadvertence the following new combinations were not legally made in the recent "Flora of the Marshes of California" by Herbert L. Mason.

ASTER OCCIDENTALIS var. *parishii* (Gray) Ferris, comb. nov. *A. fremontii* var. *parishii* Gray, Syn. Fl. N. Amer. 1 (2): 192. 1884.

ASTER OCCIDENTALIS var. *delectabilis* (H. M. Hall) Ferris, comb. nov. *A. delectabilis* H. M. Hall, Univ. Calif. Publ. Bot. 3:82. 1907.

Both of these varieties occur in California in the Sierra Nevada and in the mountains of southern California, and they reoccur in the San Pedro Martir of northern Baja California, Mexico.

Dudley Herbarium, Stanford University,
Stanford, California.

NOTES AND NEWS

Some publications of interest follow:

Under the auspices of the *Gobierno del Estado de México, Dirección de Recursos Naturales* (Toluca) publications on the *Flora del Estado de México* have continued to appear. During 1958 Professor Maximino Martínez completed the *Flora Medicinal* as well as the treatment of the Cactaceae and some forty smaller families; Professor Eizi Matuda treated the Gramineae, Umbelliferae and the Compositae.

Drawings of British Plants, by Stella Ross-Craig. Part XI. Droseraceae—Ficoidaceae. 39 pls. 1958, 9s. 6d. G. Bell and Sons, Ltd. London. Part XII. Umbelliferae (1). 36 pls. 1958. 9s. 6d. 1958.